MADROÑO

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A WEST AMERICAN JOURNAL OF BOTANY



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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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THE SIGNIFICANCE OF VEGETATIVE REPRODUCTION IN QUERCUS

CORNELIUS H. MULLER1

The regenerative powers of various species of oaks have been noted by a great many writers, but the role of rhizomatous activity has received little more than descriptive treatment incidental to taxonomic work or ecological characterization of vegetation containing scrub oaks. Jepson (1910) described stump sprouting of California oak trees at some length. Camus (1936) merely noted

its common occurrence in the genus.

Numerous authors have described briefly the rhizomatous habits of individual species. Small (1897) wrote, "The habit of Quercus minima, with its underground stems, and low erect branches which are usually much less than one meter in height, is enough to separate it specifically from the gigantic forest tree Quercus virginiana." Sudworth (1908) said of the California Quercus Breweri, "... its network of creeping roots [rhizomes], from which sucker-like stems originate, making irresistible barriers to run-off waters." Viciosa (1950), treating the Spanish species, ascribed to Quercus pyrenaica, "Roots deep, accompanied by others superficial and copiously stoloniferous about the trunk." He describes Quercus Ilex as follows: "... or a shrub, with the root system strongly and deeply developed, carrying moreover lateral and shallow roots much extended, producers of abundant retoños."

Muller (1946) pointed out the survival value of retoños in Parthenium argentatum (guayule) and that of tillers in Parthenium incanum (mariola), both of which are shrubs of semi-arid habitats in western Texas and adjacent Mexico. The tillering of mariola approaches the rhizomatous habit and sometimes produces thickets several meters in diameter, holding almost in perpetuity the site occupied by a short-lived original plant.

The rhizomatous nature of some species of Quercus has similar ecological significance, and it is furthermore on occasion a matter of great taxonomic import. It is the purpose of this paper to describe the habits of several illustrative species, to evaluate the ecological significance of the habits, and to record observations upon the taxonomic meaning of habital differences and their

evolutionary importance.

² The Spanish word retoño denotes a shoot arising from an adventitious bud on an exposed root or underground stem, usually at greater or less

distance from the trunk of the parent plant.

¹ This work was supported by a grant from the Committee on Faculty Research, University of California, Santa Barbara College. I am furthermore indebted to Dr. L. C. Hinckley, Sul Ross State College, Alpine, Texas, for his aid in the field study of Quercus Hinckleyi and for observations upon Q. Havardi in support of my own. The drawings are the work of Mr. Alan Cole.

² The Spanish word retoño denotes a shoot arising from an adventitious

Madroño, Vol. 11, No. 2, pp. 33-128. June 12, 1951.

BUSH HABIT OF QUERCUS HINCKLEYI

Quercus Hinckleyi Muller is a low shrub scarcely 0.5 meter in height. It was recently described (Muller, 1951) on the basis of the only known occurrence, a single patch of fewer than 100 plants covering less than 500 square meters at the western edge of the Solitario Basin in southeastern Presidio County in western The species is associated with sparse grasses and desert shrubs on dry slopes of thin gravelly loam in a transitional zone between grassland and desert. The habitat is distinctly arid and characterized by wide spacing of plants and infrequent establishment of seedlings of any woody species. No seedlings or even young plants of Q. Hinckleyi were found. The general region of its occurrence has been searched over a period of years by collectors of oaks so that the restriction of the species to one or a few very limited areas may be accepted as fact. Its relict nature is indicated; the existing population is likely the survival of a more extended range during less xeric periods of the recent geologic past.

The persistence of such a narrowly limited relict species immediately poses questions concerning its means of survival. The species is highly xeromorphic, its tiny leaves being thick, spiny, persistent, and heavily cutinized. Its slow growth and low stature conform with the habits of other species of arid climates where damage is inflicted upon any species whose stature over-

reaches its water supply.

The aerial stems of Quercus Hinckleyi are not long-lived. Ring counts established the largest ones at seven to nine years old. Excavations of a few shrubs revealed a distinctly rhizomatous habit involving short rhizomes. These issued as branches below the soil surface from the bases of erect stems or from older rhizomes (fig. 1) and grew laterally for distances of 4 to 15 cm. They bore reduced (scale) leaves at their nodes and lacked chlorophyll throughout. Upon reaching the soil surface, the rhizomes produced normally expanded and green leaves, and independent rooting followed within a year or two. Each individual clump was observed to consist of several to many ascending stems all springing from one or more old, thick rhizomes in a relatively small soil area, usually a circle 1 to 3 dm. in diameter. The slow spread of the rhizomes has increased the number of individuals by fracture due to death of connecting shoots.

This habit quite clearly explains the ability of the species to persist without the establishment of seedlings. Although some seedling establishment may have occurred in recent centuries, it is not necessary to assume any since the last pluvial period of the Pleistocene. In fact, the entire population is so strikingly uniform in the expression of its genetic characters that it appears almost certain that there is represented only a single clone the

age of which is very great.

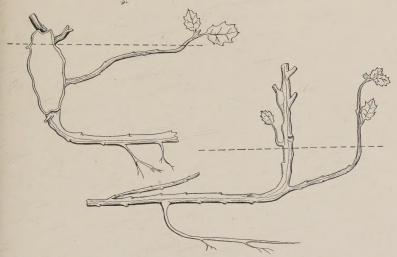


Fig. 1. Quercus Hinckleyi: single adult stems with attached rhizomes extracted from clumps.

THICKETS OF QUERCUS HAVARDI

Quercus Havardi Rydb. is the dominant of extensive shinneries³ occupying the sand hills and rolling plains of the southern Great Plains region. It ranges, wherever a deep sand substratum exists, from southeastern New Mexico across the Panhandle of Texas to southwestern Oklahoma. In addition to extensive reconnaissance, detailed observations on this species were made in Ward and Wheeler counties, Texas.

The habit of Quercus Havardi is strikingly rhizomatous. A multitude of simple or sparsely branched shoots issues from the ground and grows to a height of 3 to 8 dm. Occasional much taller individuals are of hybrid origin (Muller, 1951). Upon examination of an unbroken thicket of these shoots, it is readily determined that each arises as an elongated rhizome which assumes a vertical direction of growth upon reaching the soil surface. The rhizomes range in length from 1 to 8 or 10 dm. The vigor with which a single individual spreads its rhizomes and multiplies its aerial shoots is reflected in the large size of the resulting clones. Close attention to minor differences in color, leaf size and shape, etc. clearly reveals the limits of individual clones. These sometimes form a mosaic of patches from 3 to 15 m. or more

³ Shinnery is an adulteration of the French word chênière, still employed in Louisiana to indicate a place occupied by oaks (Penfound and Hathaway, 1938). Neither term is confined to the low shrubs referred to erroneously and redundantly as "shin-oaks" through the mistaken notion that the human tibia is somehow involved. The error is given credence through the coincidental shin-high stature of some oaks, and the adulterated term has thus been restricted in some localities to dwarf species.

in diameter, each clone in direct contact with its adjacent neighbors.

The failure of one clone to penetrate another (unless death of the plant leaves the soil unoccupied) indicates the tenacity with which the sites are held by the clones. Stems greater than 2 cm. in diameter are rare, and the greatest age revealed by terminal bud scar counts was eleven years. Individual dead shoots amongst the hundreds forming a clone are occasionally observed, but the resulting opening is so promptly closed by the growth of new shoots that ragged thickets seldom appear.

The clones of Quercus Havardi are not so luxuriant and dense where they are subject to heavy competition by grasses. The rhizomatous habit, however, spreads clones widely under these conditions also. Fracture of rhizomes under these circumstances frequently results in the division of a single clone to form several distinct individuals, sometimes eventually at some distance from

one another

In the course of a wide and detailed study of the species, Quercus Havardi was never observed to assume any habit other than a freely branching rhizomatous one. Age has no significance to an individual of this species except that it offers greater opportunity to spread and multiply by fracture. Senescence is limited to individual aerial shoots, and the entire clone is characterized by continuous rejuvenation. Seed production is usually copious, but the establishment of seedlings is rare except in disturbed areas where the young plants are relieved of competition of both the grasses and the parent shrubs. The two important consequences of the rhizomatous habit, then, are the much increased longevity of the individual and the multiplication of individuals under conditions of competition too severe for seedling establishment.

MOTTES OF QUERCUS VIRGINIANA

Quercus virginiana Mill. occurs on the coastal plain of Texas as a tree reaching great age and enormous size. Trunks 1 to 2 m. in diameter are not uncommon. It was early noted by settlers in this region that this species grew in even-aged clumps upon the rolling hills and coastal plain. Such an isolated clump of trees was termed a motte.⁴ The term is used rather indiscriminately to designate a clump of half a dozen individuals or a grove covering a half dozen acres, only the qualifying adjectives "little" and "big" being employed to distinguish such extremes. The smaller mottes are by far the most common, however, and the term has therefore gained specificity to some degree.

⁴ Motte is a French word meaning lump, clod, or hillock. The similarity of an isolated small grove of trees on a plain to such a concept led to its application. It is still being used in this sense quite correctly throughout south Texas although its origin is almost entirely forgotten.

In addition to the normally uniform trees comprising a motte, one usually observes nearby one or several patches of juvenile *Quercus virginiana* of various sizes and ages. An examination of several such patches 3 miles west of Cuero, DeWitt County, Texas, was undertaken. The soil was a rather heavy fine sandy clay loam of the Goliad series and bore a grass cover badly depleted by over-grazing. Similar patches in lightly grazed short-grass and prairie associations have been observed over a wide area in this region.

Excavation of the juvenile shoots revealed that all the shoots of a single patch were connected by an intricate system of interlacing rhizomes about 5 to 10 cm. beneath the surface (fig. 2A). In some instances the rhizomes were as much as a meter in length between organically connected adjacent aerial shoots. However, these rhizomes were criss-crossed by others which similarly bore aerial shoots so that proximity of shoots was no indication of closeness of organic connection. Yet, all the rhizomes eventually connected with one another within a single patch so that this represented a single individual (fig. 2B).

One such patch contained (1) a dead stump about 2 cm. in diameter to which two rhizomes were still attached, (2) one aerial shoot 0.5 m. in height, (3) an assortment of twenty-odd shoots ranging from a few centimeters to 2 dm. in height. Another much smaller patch contained one aerial shoot 2 dm. tall and several only a few centimeters tall. Older and larger patches formed thickets too heavy for ready excavation, but amongst shrubs 2 to 3 m. tall rhizomatously attached shoots were observed.

The patches of juvenile shoots ranged in diameter from 1 to 4 or 5 m., the larger size being correlated rather closely with the taller and older shrubs. Adjacent mottes of young trees (7 to 10 m. tall with trunks 1 to 2 dm. in diameter) had basal diameters of 2 to 6 m. Thus, an almost complete series was observed relating the juvenile patches of organically connected shoots to the adult mottes of apparently distinct trees. The isolated mottes, then, are clones derived from the rhizomatous action of seedlings (fig. 2C). The length of time such a clone remains in the shrub stage will depend upon the frequency with which aerial shoots are destroyed, mechanically or by grass fires. The resistance of the rhizomes to injury thus insures the survival of the clone through the critical period which terminates with the assumption of the tree-habit. Larger mottes are possibly formed by the confluence of adjacent small ones.

RHIZOMATOUS HABIT OF QUERCUS PYRENAICA AND QUERCUS ILEX IN SPAIN

The two common oaks north of Madrid, Spain, are Quercus pyrenaica Willd. and Q. Ilex L. In August, 1950, a visit to this area permitted a cursory examination of both species. There was no opportunity to make excavations, but several road cuts

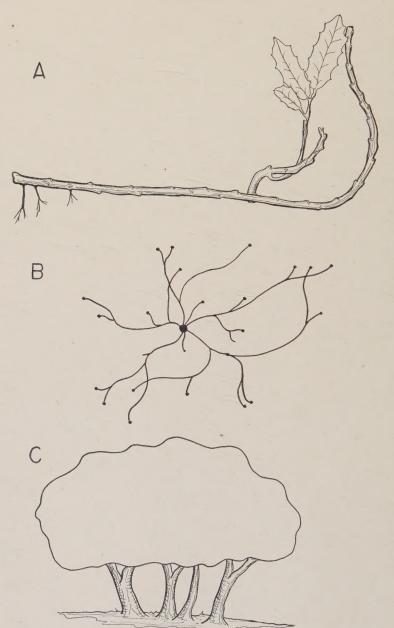


Fig. 2. Quercus virginiana: A, a portion of a juvenile rhizome exhibiting branching; B, a diagrammatic representation of the distribution of rhizomes in a single clone (the black dots indicating loci of aerial shoots); C, a small motte of young trees.

through masses of shoots were examined. These species occur abundantly on both rocky slopes and areas of flat soil. The small trees long have yielded fuel to the wood gatherers. The Spanish custom of trimming off the lower branches has spared many of these trees until senescence and repeated injury finally killed the trunks. Meanwhile, however, the partially or wholly decapitated trees have produced large numbers of shoots from the base of the trunk as well as at some distance from the trunk. Although Quercus Ilex was observed to produce more numerous shoots covering a greater area about the stump or trunk than Q. pyrenaica, and Q. pyrenaica sometimes produced clumps of trunks rather than single trunks, the two species are so similar in respect to the sprouting habit that they may be discussed jointly.

Where the trees occurred on eroded slopes it is likely that at least some of the sprouts arose as retoños induced by injury to exposed roots. However, the numerous individuals observed on level and undisturbed soil could not have experienced such root injury. Similarly, although felled and partially decapitated trees would be expected to produce stump sprouts as described by Jepson (1910) for so many of their California relatives, the many undisturbed mature trees observed in Spain exhibiting a wide circle of shoots at some distance from their bases are not of this class. The road cuts examined showed clearly the rhizomatous connections between individual shoots of various sizes and established the origins of these. This instance, then, is entirely comparable to the rhizomatous spreading commonly observed in Quercus Breweri of California and numerous other species. It differs principally in the fact that the rhizomatous shoots of Q. pyrenaica and Q. Ilex are produced after tree habit is assumed.

DISCUSSION

It is clear from the cases described that the various species of Quercus differ widely in the form of rhizomatous sprouting exhibited. Four general classes (exclusive of stump sprouting) have been described as follows: (1) short rhizomes in Q. Hinckleyi, (2) long rhizomes in Q. Havardi, (3) juvenile rhizomes of long duration terminated by tree-habit in Q. virginiana, and (4) rhizomes from mature trees in Q. pyrenaica and Q. Ilex. Although usually only one example was described in each of the four classes, it is noteworthy that one form or another of the rhizomatous habit is demonstrable in a wide variety of shrubby American species. A few of these are Q. Breweri Engelm., Q. dumosa Nutt., Q. Gambelii Nutt., Q. Mohriana Rydb., Q. oleoides var. quaterna Muller, Q. pungens Liebm., Q. pungens var. Vaseyana (Buckl.) Muller, Q. turbinella Greene, Q. undulata Torr., and Q. vaccinifolia Kellogg, all in the Southwestern United States (from Texas to California). Scores of Mexican and several Atlantic region species might be added to the list.

The ecological significance of clonal spread is great in any semi-arid region unfavorable to seedling establishment. Not only is reproduction and invasion thus accomplished without the aid of the hazardous seeding process, but rejuvenation of short-lived individuals may thus be prolonged indefinitely. This increase in longevity is particularly important where competition with more xerophytic forms is intense. In this connection, it is noteworthy that in semi-desert regions the common woody associates of rhizomatous Quercus species with rare exceptions also exhibit the bush habit and rejuvenation by sprouting.

The exceptionally wide geographic occurence of the rhizomatous habit coincides significantly with the semiarid climates of the regions involved. Although wide variations in climate exist amongst central Spain, western Texas, and southern California, they are all characterized by long periods of deficient soil moisture in summer. However, there exist outstanding exceptions to this coincidence of the rhizomatous habit of oaks with semi-arid climate. Notable amongst these are Quercus minima on the sandy coastal plain in Florida, Q. Margaretta Ashe on sand beds of the Gulf coastal plain, and Q. ilicifolia Wang. confined to sandy barrens and rocky hills in the northeastern United States. It must be emphasized, however, that the number of species constituting such exceptions is small and that the plants involved are confined largely to edaphically adverse habitats.

In problems of taxonomic use of habital differences, the life history of the plant may be of distinct importance. Small's distinction of Quercus minima from Q. virginiana quoted above may or may not have been justified, but his employment of habit was unfortunate. The elements of the life history of Q. virginiana here described would cast doubt upon the taxonomic significance of

habit in the southern live oaks.

An equally important significance of the rhizomatous habit is the role of the resulting longevity in determining evolutionary rate. Genetic processes of definite rate operate in a breeding population to a degree proportional to the frequency of sexual reproduction. Apomictic behavior in vegetatively reproducing clones is no different in this respect from apomictic seed production and results in a similar marked depression of sexual frequency. Thus, long-lived clones can serve to preserve a population in which a genetic difference has arisen or they can so restrict the rate of introgression as to postpone indefinitely the swamping of one species by another.

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A NEW FRITILLARIA FROM OREGON

HELEN M. GILKEY

In southwestern Oregon and northwestern California—that area known by all West Coast taxonomists as rich in endemics—one of the most conspicuous wayside flowers is that of the "red bell", "red lily", or "scarlet fritillary", Fritillaria recurva Benth. No species of this genus thus far described from Western America approaches it in brilliance of color.

In 1941, however, Mr. L. G. Gentner, entomologist and assistant superintendent of the Southern Oregon Branch Experiment Station at Medford who, with his wife and two daughters perhaps comes nearer knowing every inch of Jackson and Josephine counties with their insects and plants than any other person in the state, reported what appeared to him an undescribed species of Fritillaria. The previous year his daughter Laura had brought in for her garden a plant supposed to be the common "red bell", but which, when it flowered, was noticeably different from F. recurva. The area, however, from which it had been collected was by this time forgotten. Numerous trips were made by the family in an endeavor to find the plant, but not until Katherine, another daughter, recognized the new lily in a flower arrangement at the home of a friend, was the original location rediscovered in the vicinity of Jacksonville.

As brilliant in color as *F. recurva*, the blossom of this new form is consistently of a different shade of red; its flowering period begins two weeks later; the plant is typically more robust; and the flower shape so different that regardless of other dissimilarities, plants of the two entities can readily be distinguished from a car moving rapidly on the highway.

Since the first report, it has been possible to make intensive studies of plants of both forms in all stages, not only in the field and from generous collections provided by Mr. Gentner, but also from plants grown at the Oregon State College Herbarium and in the Gentner garden. As a result of these studies, the "new" form appears, in the morphology of the flower as well as in the superficial aspects of the plant previously mentioned, so distinctly

different from any species thus far described, as to merit specific rank and recognition. It is a pleasure, therefore, to describe this beautiful species and to perpetuate in it the name of the family who discovered it. Colors indicated in the English diagnosis are from Ridgway's Chart.

Fritillaria Gentneri sp. nov. Caulis robustus 3-6 dm. altus, folia glauca lanceolata obtusa ad linearia acuta 7-15 cm. longa 0.7-1.5 cm. lata, flores 1-5 (raro 8 vel 9) pedicellis gracilibus, perianthium infundibuliformum vel campanulatum puniceum sanguineum rubiginosum vel purpureum maculis pallidis luteis notatum segmentis 3.5-4 cm. longis apicibus haud recurvatis glandulis conspicuis, capsula 2-2.5 cm. longa 2.5-3.5 cm. lata late alata.

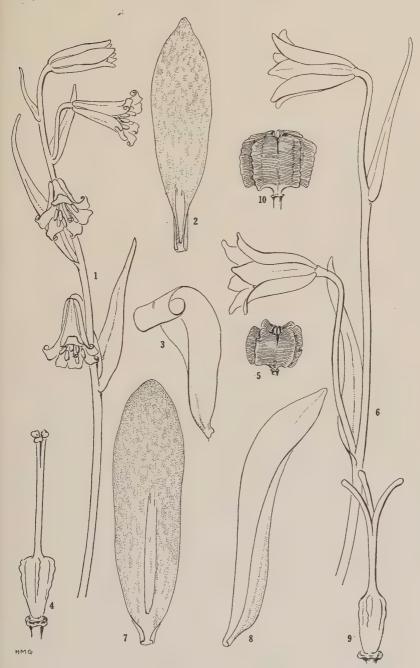
Bulb fleshy, the axis wide and flattened vertically in older specimens, with several large fleshy scales surrounded by numerous small rice-grain scales; stem typically robust, 5-7 dm. (measured from bulb to tip), reddish below ground line, glaucous green to glaucous purple above, or minutely purple-mottled; leaves generally lanceolate, sometimes broadly linear, 7-15 cm. long, 0.7-1.5 cm. broad near base, often in 2 whorls of 3 and sometimes with a pair of one or 2 alternate leaves above, but in larger specimens frequently with 5 to a whorl and several extra leaves above or between whorls; flowers solitary or often in bracted racemes, 1-5 (rarely 8 or 9), on long slender pedicels; perianth infundibuliform to campanulate, 3.5-4 cm. long, the segments overlapping, with somewhat spreading but not recurved tips, varying through Carmine, Oxblood Red, Maroon, Purple, mottled with pale yellow, segments keeled beneath by presence of deep and conspicuous glands; stamens included; style generally reaching anther tips, branches split nearly one-half the length of the style, spreading, stigmas inconspicuously capitate; capsule truncate or rounded at apex, truncate to slightly cordate at base, reaching 2-2.5 cm. in length, 2.5-3.5 cm. in width, broadly winged, the wings dentate.

Type. Vicinity of Jacksonville, Jackson County, Oregon, 19 April 1950, Gentner and Gilkey (Oregon State College no. 75839). Known additional locations. Jackson County: near State Highway 238, 6 miles southwest of Jacksonville; Holcomb Springs, 15 miles northwest of Jacksonville; Murphy. Josephine County: near Grants Pass.

This species, because it is "red", is most likely to be confused superficially with *F. recurva* to which it is perhaps most closely related. The points clearly differentiating the two are indicated

EXPLANATION OF FIGS. 1-10.

Figs. 1-5. Fritillaria recurva: 1, flowering stalk, $\times 2/3$; 2, outer perianth segment, face view, $\times 2$; 3, outer segment, profile to show short gland, $\times 2$; 4, pistil, $\times 2$; 5, capsule, $\times 2/3$. Figs. 6-10. Fritillaria Gentneri: 6, flowering stalk, $\times 2/3$; 7, outer perianth segment, face view, $\times 2$; 8, outer segment, profile, showing long gland, $\times 2$; 9, pistil, $\times 2$; 10, capsule, $\times 2/3$.



Figs. 1-10. Fritillaria recurva and F. Gentneri.

in the illustrations and in the table in which flower characters are compared.

COMPARISON OF FLOWER CHARACTERS IN FRITILLARIA GENTNER! AND F. RECURVA						
	F. <u>Gentneri</u>	F. recurva				
Shape	Broadly campanulate; perianth segments oblanceolate, obovate, or oblong, tapering gradually downward, overlapping, somewhat spreading at tips but not recurved.	Narrow, perianth segments oblanceolate or obovate, tapering quite abruptly downward, tending to separate for nearly entire length, strongly recurving at tips.				
Basic color of perianth		Jasper Red, Scarlet Red, Scarlet, Nopal Red—all "yellowish" shades of redto Pale Orange-Yellow or Chamois.				
Gland	Conspicuous, extending half the length of the segment, forming a conspicuous keel on the dorsal surface.	Extending one-fourth the length of the segment or less.				
Stamens	Generally equaling the pistil in length, not conspicuously exposed by recurving of perianth.	Generally exceeding the pistil, con- spicuously revealed by recurving of perianth.				
Style branches	Equaling nearly half the length of the style, widely spreading.	Equaling less than one-fourth to one-third the length of the style, erect or nearly so.				

Fritillaria recurva Benth. var. coccinea Greene with perianth segments generally not recurved, and with fewer bulb scales, otherwise has F. recurva characteristics, its color being an even more vivid scarlet.

Comparison of F. Gentneri was made also with F. adamantina Peck (1937) which is described as "reddish" ("pale reddish mottled with deeper purplish spots." Peck). The type specimen, located in the Peck Herbarium at Salem, Oregon, as well as fresh plants collected by Mr. Gentner in the type locality (Diamond Lake, Oregon) were consulted, and indicated no close relationship between the two. In the present author's opinion, F. adamantina presents a closer kinship to the F. lanceolata complex or, according to Dr. Peck (1937), to F. multiflora, than to either F. Gentneri or F. recurva, as suggested by Mrs. Beetle (1944); and it cannot from any point of view be confused with either of the latter.

Fritillaria Gentneri forms almost a pure stand in its type locality and in several other areas from which it is known. In some cases, however, it overlaps with F. recurva, but there is no indication of intermediate forms. The species is remarkably constant in size and color. Fritillaria recurva, on the other hand, is widely variable, but deviations in color are never in the direction of F. Gentneri.

Unfortunately, in most species of Fritillaria, color characters become considerably obscured by drying; and in pressed specimens it is sometimes difficult to distinguish boundaries of glands,

however conspicuous they may be in fresh material. In the case of F. recurva and F. Gentneri, however, pistil characters and flower shape can be relied upon for diagnosis under any conditions thus far encountered.

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A CYTOTAXONOMIC APPROACH TO ESCHSCHOLTZIA

HARLAN LEWIS AND RICHARD SNOW

The genus Eschscholtzia has received varied taxonomic treatments during the last half century, ranging from the recognition of over 100 Californian species by Greene (1905) and Fedde (1909) to seven by Jepson (1925). There is good reason to believe that neither of these extremes represents the actual situation. We wish here, however, only to indicate the important contributions that cytological observations can make to an understanding of the relationships and to the delimiting of species within this genus.

One example concerns Eschscholtzia minutiflora Watson and E. Parishii Greene. E. minutiflora is widespread over both the Colorado and Mohave Deserts, and extends into Baja California, Arizona, Nevada, and southern Utah. It is variable throughout this range, but can usually be recognized most readily by its small flowers (petals less than 8 mm. long), and short-apiculate buds. The stamens number about 12, with anthers about as long as the filaments.

Eschscholtzia Parishii, listed in current manuals as a variety of E. minutiflora or as a synonym of E. minutiflora var. darwinensis Jones, has a more restricted range than E. minutiflora. It occurs

throughout the Colorado Desert and on the southern margin of the Mohave Desert. Over its entire range it is sympatric with *E. minutiflora* and the two can often be found growing side by side. The distinguishing features are its much larger flowers (petals up to 23 mm. long) and long-apiculate buds. The stamens are about twice as numerous in this species, and the anthers are often longer than the filaments. On the whole, *E. Parishii* is much more variable than *E. minutiflora*.

When these two entities grow side by side, they are completely distinct morphologically and show no evidence of hybridization. Furthermore, observations of pollen mother cells have shown that *E. Parishii* has 6 pairs of chromosomes, while *E. minutiflora* has 18 pairs and is therefore a hexaploid. Thus there is no doubt as to the nature of the barrier restricting gene recombina-

tion between these two species.

These two species, then, are apparently genetically isolated and morphologically distinct when found growing together. Nevertheless, a study of herbarium material collected over a great many years, and from a variety of localities, shows that many morphological intermediates do occur between these two species. It is presumably because of these intermediates that some authors have considered these two entities to be conspecific. Lewis and Went (1945) have shown, however, that certain species of Eschscholtzia, when grown under controlled conditions, can be modified by the external environment both as to flower size and vegetative characters. Similar modifications have also been observed by Jepson (1922). Thus it would seem probable that environmental modification is primarily responsible for the intermediate phenotypes which obscure the genetic discontinuity between E. minutiflora and E. Parishii.

The plant described by Jones in 1898 as E. minutiflora var. darwinensis further complicates the picture. This entity occurs in the Mohave Desert, principally in the Panamint, Funeral, and White mountains, and is also sympatric with E. minutiflora. It scarcely overlaps the range of E. Parishii, if at all. In several respects, notably in flower size, it is intermediate between E. Parishii and E. minutiflora. It appears morphologically quite homogeneous, however, and may well represent a third species, possibly a tetraploid, which in combination with E. Parishii may have given rise to the hexaploid E. minutiflora. Unfortunately, we have not as yet been able to obtain material for chromosome counts or

experimental studies.

Eschscholtzia californica and E. caespitosa have been previously reported to have a haploid chromosome number of 6 (Darlington and Janaki-Ammal, 1945), and our observations of E. caespitosa are in agreement. Thus 6 is apparently the basic number in this

¹ Material has been borrowed from Pomona College and the University of California, Berkeley. The authors wish to thank the curators of these herbaria.

genus. However, an examination of the pollen mother cells of E. glyptosperma Greene has shown that it has a haploid number of

7, a number new to this genus.

All of the problems in Eschscholtzia cannot be solved by cytological observations, but these examples indicate that they will prove to be of great value in indicating specific limits in this genus.

SPECIMENS EXAMINED CYTOLOGICALLY

E. caespitosa: Davy Brown Camp, San Rafael Mts., Santa Barbara Co. Lewis, April, 1950.

E. glyptosperma: Silver Lake-Cave Springs road, Avawatz Mts., San Bernar-

dino Co. Ball 716.

E. minutiflora: U. S. Highway 60, 5 mi. west of road to Cottonwood Springs, Riverside Co. Lewis and Ernst, March 26, 1949. 1 mi. south of Atolia, San Bernardino Co. Lewis, April 1950.

E. Parishii: U. S. Highway 60, 5 mi. west of road to Cottonwood Springs, Riverside Co. Lewis and Ernst, March 26, 1949. Joshua Tree National Monu-

ment. Lewis, April, 1949.

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LITERATURE CITED

DARLINGTON, C. D. and E. K. JANAKI-AMMAL. 1945. Chromosome Atlas of Cultivated Plants. London.

Fedde, F. 1909. Papavaraceae in A. Engler, Das Pflanzenreich. IV (104): 144-202. Leipzig.

NOMENCLATURAL RECOMBINATIONS IN IDAHO PLANTS

RAY J. DAVIS

Looking forward to the publication of a "Flora of Idaho" this summer (1951), I am making the following nomenclatural recombinations separate from this book.

ERYTHRONIUM GRANDIFLORUM Pursh var. idahoense (St. John & G. N. Jones) comb. nov. E. idahoense St. John and G. N. Jones,

Res. Stud. St. Coll. Wash. 1: 91. 1929.

Eriogonum caespitosum Nutt. var. acaule (Nutt.) comb. nov.

E. acaule Nutt. Jour. Acad. Phila. Ser. 2, 1: 160. 1848.

POLYGONUM BUXIFORME Small var. montanum (Small) comb. nov. P. douglasii montanum Small, Mem. Dept. Bot. Columbia Coll. 1: 118. 1895.

POLYGONUM HETEROPHYLLUM Lindm. var. rubescens (Small) comb. nov. P. rubescens Small, Bull. Torrey Club 33: 56. 1906.

Claytonia fontana (L.) comb. nov. Montia fontana L. Sp. Pl.

87. 1753.

ARENARIA CAPILLARIS Poir. var. americana (Maguire) comb. nov. A. capillaris Poir. subsp. americana Maguire, Bull. Torrey Club 74: 41. 1947.

Delphinium Andersoni Gray var. cognatum (Greene) comb.

nov. D. cognatum Greene, Pittonia 3: 14. 1896.

DELPHINIUM DIVERSIFOLIUM Greene var. Harneyense (Ewan) comb. nov. D. diversifolium Greene subsp. Harneyense Ewan, Univ. Colo. Stud. D. 2(2): 115. 1945.

Delphinium occidentale (Wats.) Wats. var. cucullatum (Nels.) comb. nov. D. cucullatum A. Nels. Bull. Torrey Club 27:

262. 1900.

ERYSIMUM CAPITATUM (Dougl.) Greene var. amoenum (Greene) comb. nov. Cheiranthus nivalis amoenus Greene, Pittonia 3: 137. 1896.

ERYSIMUM CAPITATUM (Dougl.) Greene var. argillosum (Greene) comb. nov. Cheiranthus argillosus Greene, Pittonia 3: 136. 1896.

ERYSIMUM CAPITATUM (Dougl.) Greene var. perenne (Wats.) comb. nov. E. asperum var. perenne S. Wats. ex Coville, Proc. Biol. Soc. Wash, 7: 70. 1892.

Amelanchier alnifolia Nutt. var. oreophila (A. Nels.) comb.

nov. A. oreophila A. Nels. Bot. Gaz. 40: 65. 1905.

Fragaria virginiana Duchesne var. ovalis (Lehm.) comb. nov. Potentilla ovalis Lehm. Delect. Sem. Hort. Hamb. 1849: 9. 1849.

Fragaria vesca L. var. bracteata (Heller) comb. nov. F. bracteata Heller, Bull. Torrey Club 25: 194. 1898.

Providenta Heller, Bull. Forrey Chib 25: 194. 1898.

Rubus idaeus L. var. melanolasius (Focke) comb. nov. R. melanolasius Focke, Abh. Naturw. Ver. Bremen 13: 469. 1896.

Lathyrus Pauciflorus Fern. var. utahensis (Jones) comb. nov. L. utahensis Jones, Proc. Calif. Acad. Ser. 2, 5: 678. 1895.

LUPINUS ARGENTEUS Pursh var. Macounii (Rydb.) comb. nov.

L. Macounii Rydb. Bull. Torrey Club 34: 42. 1907.

OXYTROPIS BESSEYI (Rydb.) Blank. var. argophylla (Rydb.) comb. nov. Aragallus argophyllus Rydb. Mem. N. Y. Bot. Gard. 1: 255. 1900.

Oxytropis campestris (L.) DC. var. Cusickii (Greenm.) comb. nov. O. Cusickii Greenm. Erythea 7: 116. 1899.

Oxytropis campestris (L.) DC. var. Rydbergii (A. Nels.) comb. nov. O. Rydbergii A. Nels. Univ. Wyo. Publ. Bot. 1: 117. 1926.

VIOLA PALUSTRIS L. var. brevipes (Baker) comb. nov. V. palustris L. subsp. brevipes Baker, Madroño 3: 235. 1936.

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A NEW ARTEMISIA FROM WYOMING

ARTHUR CRONQUIST

Artemisia Porteri sp. nov. Herba perennis Artemisiae pedatifidae similis et vix altior sed tomento densiore argentiore in omnibus partibus robustior, foliis 2–5 cm. longis laminis vel segmentis 1–4 mm. latis, caulinis et nonnullis imis integris reliquis ternatis segmentis 1–2 cm. longis, involucris 5–7 mm. altis, bracteis 12–15, floribus femineis 8 vel 9–10, corollis 2.1–2.8 mm.

longis, disci floribus 22-32, corollis 4-4.5 mm. longis.

Taprooted, mat-forming perennials with numerous slender annual stems 7-15 dm. tall; herbage closely sericeous-tomentose, silvery; leaves 2-5 cm. long, the larger basal ones trifid, the rest mostly entire, the blade or segments 1-4 mm. wide, the segments 1-2 cm. long; heads several in a relatively long and narrow, leafy-bracteate, subracemiform inflorescence, the terminal head similar to the lateral ones; involucre 5-7 mm. high, of 12-15 bracts; receptacle glabrous; marginal flowers commonly 8, sometimes 9 or 10, pistillate, fertile, with tubular corolla 2.1-2.8 mm. long; central flowers 22-32, staminate, with abortive ovary, the corolla 4-4.5 mm. long.

Type. Plants very aromatic, forming mats on dry, loose shaley soil in the desert about 10 miles east of Sand Draw Oil Field and 40 miles southeast of Riverton, Fremont County, Wyoming, 6000 feet, July 6, 1949, C. L. Porter 4969 (Rocky Mountain Herbarium 214909). Isotypes at the State College of Washington, University of Washington, Gray Herbarium of Harvard University, Canadian Dept. of Agriculture (Ottawa), Academy of Natural Sciences of Philadelphia, Dudley Herbarium of Stanford University, New York Botanical Garden, California Academy of Sciences, University of Colorado, Missouri Botanical Garden, University of Oklahoma, University of California (Berkeley), and

U. S. National Herbarium.

Artemisia Porteri is obviously related to A. pedatifida Nutt., but is larger and more robust throughout. Artemisia pedatifida, generally distributed over the high plains and dry hills of Wyoming, and extending into Carbon County, Montana, shows so little variability that all of the 20 collections I have examined could easily pass for parts of a single colony. Artemisia Porteri is so far known only from a single extensive and uniform collection from central Wyoming, where it grows with A. pedatifida without intergradation. If further collections prove it to be anywhere nearly as constant as A. pedatifida, there need never be any difficulty in distinguishing the two at a glance. Of the technical characters, the number and size of the disk-flowers seem to be among the most solid. The more obvious differences are listed in the following table.

A. pedatifida

A. Porteri

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Pubescence grayer, less dense, and less silvery.

All or nearly all of the basal leaves

trifid.

At least some of the cauline leaves trifid.

Leaves 6-20 mm. long.

Leaf-segments less than 1 cm. long. Involucre 3-4 mm. high.

Involucral bracts 7–13, typically 8. Pistillate flowers 3–8, typically 5, with

corolla 1.3-1.7 mm. long.

Disk-flowers 5-15, typically 8 or 9
(larger numbers usually on terminal heads), with corolla 2.8-3.5
mm. long.

Pubescence denser, tighter, and more silvery.

Many of the basal leaves entire.

Cauline leaves all or nearly all entire. Leaves 2-5 cm. long.

Leaf-segments 1-2 cm. long. Involucre 5-7 mm. high.

Involucre 5-7 mm, mgn.
Involucral bracts 12-15.
Pictillete flowers mostly 8

Pistillate flowers mostly 8, sometimes 9 or 10, with corolla 2.1-2.8 mm. long.

Disk-flowers 22-32 (terminal heads similar to the lateral ones), with corolla 4-4.5 mm. long.

Although the lateral heads of A. Porteri are ordinarily similar in size to the terminal head, a single head which had obviously been dwarfed by its immediate juxtaposition to a terminal head was dissected in an effort to determine extreme limits of variation. It had 11 involucral bracts, 6 pistillate flowers, and 16 disk-flowers, in these respects coming at about the upper limits for A. pedatifida; the corollas of both the pistillate and the sterile flowers, however, were of normal size for A. Porteri.

Although no definite information is available, it seems possible that A. Porteri is an autoploid derived from A. pedatifida. Whatever its mode of origin, A. Porteri is so far beyond the limits of variation of A. pedatifida as to demand taxonomic recognition.

Artemisia Porteri is named for its collector, who sent it to me as probably representing a new species.

State College of Washington Pullman

A NEW GENUS OF ECUADOREAN ARACEAE

ALEX D. HAWKES

Recently, through the courtesy of Dr. Harold N. Moldenke of the New York Botanical Garden, the writer received a small packet of araceous plants for routine determination. Among these was a single sheet of a small, apparently terrestrial aroid from Eucador, which, upon study, proved to be unreferable to any established genus. It forms the subject for the present paper.

The new genus, proposed herein as Pseudohomalomena, is a member, under the Englerian system of classification (Engler and K. Krause. Homalomeninae und Schismatoglottidinae. Das Pflanzenreich IV^{23Da}. 1912. Leipzig) of the Subfamily Philoden-

droideae, Tribe Philodendreae, Subtribe Homalomeninae, and is closest to *Chamaecladon* Miq. in its characteristics, though standing virtually alone in the subtribe because of its extraordinary spathe.

Pseudohomalomena, gen. nov. Herba terrestris verisimiliter acaulis. Petiolus folio brevior inferne leviter vaginatus. Lamina glabra erecta hastata longo-attenuata coriacea apice caudata margine undulata basi cordata, costa media subtus distincta supra obscura, nervis primariis adscendentibus ad marginem versus obscura. Pedunculus longus obscure angulatus sulcatusque valde divergens. Spatha magna planiuscula ovato-triangularis longo-caudata margine leviter undulata basi introrsa prominente nervosa chartacea. Spadix spatha brevior sessilis inflorescentia femina cylindroidea tertiam partem totius longitudinis aequante, masculina tota fertilis eae feminae arcte contigua. Flores unisexuales nudi, ei masculini truncati 2-5-andri, pistillati globosi vel urceolato-globosi obscure sulcati apice attenuati stigma unica orbiculari basi gracili plerumque obscure bilobata staminodio 1-3 ad basin florium pistillatorum inserto filamento gracili ovulis pluribus parietalibus pendulis.

Pseudohomalomena pastoensis sp. nov. Herba terrestris magna. Folium 29 cm. longum basi 15.5 cm. latum medio 12 cm. latum prope apicem 3.5 cm. latum, nervis primariis utrinsecus plus minusve 8, nervis secondariis prominentibus leviter anastomosantibus adscendentibus. Pedunculus 12 cm. longus medio 5 mm. latus. Spatha "lutea quasi alba basi virens" 22 cm. longa usque ad 14.75 cm. lata. Spadix "auranteo-luteus" plus minusve 8.5 cm. longus, basi 1 cm. latus apice 4 mm. latus, inflorescentia femina

2.5 cm. longa.

Terrestrial, rather large herb, apparently stemless. Leaf erect, glabrous, the lamina hastate, long-attenuate, coriaceous, probably yellowish-green with a darker orbicular area at basal center, 29 cm. long (counting the caudate apex, which in our specimen measures ca. 1.5 cm. in length), 15.5 cm. broad at base, 12 cm. wide at middle and 3.5 cm, near apex, base cordate, tightly undulate marginally; nerves more prominent below than above, the primaries about 8 on each side of the midrib, ascending marginally, the secondaries prominent, scarcely anastomosing, ascending. Petiole shorter than leaf, 13.5 cm. long, 1.2 cm. broad at base, narrowing to 6 mm. in middle and then expanding at leaf-junction to 1 cm., obscurely striate, probably terete and somewhat laterally compressed, conduplicate apically and vaguely undulate there. Peduncle curving, erect, spreading basally, ca. 12 cm. long, 5 mm. broad at middle, sparsely sulcate. Spathe "bright vellow, almost white, green basally" (fide collector), large, very spreading, nearly flat, ovate-triangular in general outline, chartaceous, long-caudate, rough-textured, slightly undulate marginally, the basal parts introrse, very prominently nervose throughout, obscurely and irregularly so within, 22 cm. long (counting the caudate apex,



Fig. 1. Pseudohomalomena pastoensis gen. and sp. nov.: 1, leaf, spathe and spadix, all $\times \frac{1}{2}$; 2, single pistillate flower, cut open to show parietal placentation of the ovules, $\times 8$; 3, two staminodia at base of pistillate flower, $\times 3$. Drawn by the author.

which measures 4 cm. long and averages 1 mm. wide), 14.75 cm. wide at largest point. Spadix rigidly erect, "orange-yellow" (fide collector), about 8.5 cm. long, 1 cm. wide basally, narrowing to 4 mm. wide at apex, the basal 2.5 cm. composed of pistillate flowers, irregularly furnished with staminodes, the upper part all fertile, staminate; pistillate flowers globose to urceolate-globose, obscurely sulcate, slightly attenuated apically, surmounted by a solitary orbicular stigma which is narrowed basally and often obscurely bilobate, with 1-3 staminodes on slender filaments around base; ovules parietal, pendulous, few (4-5) in number. Staminate flowers contiguous with pistillate ones, truncate, with 2-5 stamens, producing very copious yellowish-white pollen.

Type. Pasto, altitude about 2500 m., Ecuador, April 22, 1950, Reinaldo Espinosa 2866 (Herbarium of the University of California,

no. 905798).

The genus *Pseudohomalomena* is virtually unique in the subtribe Homalomeninae in its widely-spreading, almost flattened, large spathe. The dimensions of this structure, coupled with the relatively small size of the spadix and the unusual vegetative habit, set the genus apart from its congeners, *Chamaecladon Miq.*, *Curmeria Lind. & Andre, Diandriella Engl. and Homalomena Schott.*

The writer wishes to express his appreciation to Dr. Rimo Bacigalupi for assistance in the preparation of the Latin diagnoses.

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REVIEWS

Families of Dicotyledons. By Alfred Gundersen. The Chronica Botanica Company, Waltham, Massachusetts. xvii + 237 pp., illustrated. 1950. \$4.50.

Alfred Gundersen was born in 1877. In 1914, after due academic training, he joined the staff of the Brooklyn Botanic Garden, in which institution he served for thirty-two years, at first as an assistant in the herbarium, later as Curator of Plants. The treatments of the classification of dicotyledons by Rendle, 1925, and Hutchinson, 1926, interested him in the studies of which the results are presented in the work here under discussion. This work is the continuation of a memorable series, extending back at least to Caesalpino, and it is at the same time the crowning and worthy achievement of one man's life.

Training, ability, and industry are evident throughout. Index and bibliography are duly provided. The illustrations are abundant, informative, and attractive. The publishers, the Chronica Botanica Company, have treated the publication as though with individual loving care.

Gundersen arranges and names the orders and blocks of orders of dicotyledons as follows:

		MAGNOLIFLORAE		
1.	Magnoliales	2. Ranales	3.	Piperales
		CISTIFLORAE		
1.	Cactales	4. Papaverales		Aristolochiales
-	Cistales	5. Sarraceniales	7.	Tamaricales
3.	Salicales	m		
		THEA GROUP	9	Ericales
1.	Theales	2. Ebenales	ð.	Ericales
		Rosaeflorae		
	Rosales	3. Thymelaeales	4.	Myrtales
2.	Hamamelidales			
		ULMUS GROUP	0	T. Hussialan
	Proteales Santalales	4. Balanopsidales5. Fagales		Leitneriales Casuarinales
	Urticales	o. ragales	٠.	Casuarmaics
υ.	Criticales	MALVA GROUP		
1	Malvales	2. Euphorbiales		
1.		GERANIUM GROUP		
1	Rutales	3. Sapindales	5	Geraniales
	Juglandales	4. Celastrales	υ.	Octamates
	8	DIANTHIFLORAE		
1	Caryophyllales	3. Primulales	4	Plantaginales
	Polygonales	o. Tillimulaies	T.	Tantaginates
		JASMINIFLORAE		
1.	Loganiales	3. Boraginales	4.	Campanales
	Polemoniales			1
		RUBIFLORAE		
1.	Umbellales	2. Rubiales	3.	Asterales

Diels, editing Engler's Syllabus in 1936, recognized 44 orders and 257 families of dicotyledons. Gundersen has combined more often than he has divided, and has produced a list of 42 orders and 240 families. He leaves only seven orders which consist of single families.

Conforming to current practice, Gundersen has applied a uniform termination to the names of orders. Assuming that this practice is not yet so firmly established as to be beyond debate, one may say that it is no compliment to the intelligence, and that it flies in the face of priority.

In his concluding remarks, Gundersen proposes the establish-

ment by international action of an official sequence of families. This project is not feasible, for the reason that fixing the sequence of families would have the effect of classifying them. Classification, in contrast to naming, is not subject to legislation: its ultimate authority is not human will, but human knowledge.

The reviewer was honored to be one of a number of botanists whom the author admitted to smaller or greater degrees of collaboration. While accepting this honor, he reserved the right to criticize. In dealing with personal opinions and contributions, discourse in the first person will be permissible. Probably it was by my own carelessness in reading manuscript that I find myself saying, on page 18, that the nucleus of the pollen grain undergoes meiosis. Of course, it is the nucleus of the pollen mother cell that

undergoes this process.

Placentae which are axile at anthesis are regularly parietal during early development. Gundersen concludes that parietal placentation is relatively primitive. He assembles under the name of Cistiflorae several orders which exhibit this character, and gives them an early place in the sequence of orders. I called it to his attention, that the parietal placentation of certain monotropoid genera is apparently derived; but I was unable to cite any principle in conflict with the classic biogenetic doctrine which guided him. Recently I have found writers, particularly zoologists, making much of paedomorphosis, that is, of courses of evolution by which the juvenile condition of particular groups becomes the adult condition of derived groups. Assuming that paedomorphosis is prevalent, it is not probable that parietal placentation is the mark of one primitive natural group.

I attribute to myself much responsibility for Gundersen's Thea Group. Dr. Gunderson required of me a full exposition of the grounds for placing Ericales next to Theales. It was possible to answer him by citation of authority, from Lindley to Schnarf, and by a comparison of characters, of wood, of flowers, and of embryogenic stages. The purpose of the foregoing statement is not personal publicity; it is to show by example the procedure which is necessary in attaining a taxonomic system truly representative of nature. It is only by group-by-group study that the true system can be approached. There is only one condition under which one can attain confidence in a hypothesis that certain groups belong together. The condition is this, that a considerable number of pieces of evidence, of varied character, are found uniformly to tend to support the hypothesis in question. It is on this basis that I warrant Gundersen's Thea Group as essentially sound.

Various other novel arrangements presented by Gundersen appear happy. The community of plant taxonomists is called upon to judge them: each taxonomist is to give judgment upon those details which he is individually qualified to judge.—Herbert F. Copeland, Sacramento College, Sacramento, Cali-

fornia.

NOTES AND NEWS

As a memorial to the late Willis Linn Jepson, Professor of Botany at the University of California, founder of the California Botanical Society, and one of California's foremost botanists and proponents of conservation, a large grove of Bishop pines (Pinus muricata) is to be included in the proposed state park on the shores of Tomales Bay in Marin County, California. The Marin Conservation League, which, under the leadership of Mrs. Norman B. Livermore has been instrumental in furthering the establishment of this area as a state park, has agreed to raise the final \$10,000 required for the purchase of the property. As has been the case in the establishment of many other state parks, the State will match funds raised for the purchase of this land. Contributions will be accepted by the League's Treasurer, Elmer Nielsen, at the American Trust Company in San Rafael. The site of the proposed park is one of the most picturesque coastal regions of California. We should welcome the opportunity to help preserve such an area.

We call to your attention the following recent publications. Illustrated Flora of the Pacific States, by LeRoy Abrams. Volume three, Geraniaceae to Scrophulariaceae. Stanford University Press, Stanford, California. 866 pp., illustrated.

The Cacti of Arizona, by Lyman Benson. Second edition. University of Arizona Press, Tucson. 134 pp., illustrated. 1950.

Gray's Manual of Botany, by M. L. Fernald. Eighth edition. American Book Company. 1632 pp., illustrated. 1950. \$9.50.

Annotated Distributional List of the Ferns and Flowering Plants of San Diego County, California, by Ethel Bailey Higgins. Occasional Papers, San Diego Soc. Nat. Hist., No. 8, San Diego, California. 174 pp. 1949. \$1.25.

Manual of the Grasses of the United States, by A. S. Hitchcock. Second edition, revised by Agnes Chase. U. S. Dept. Agr. Misc. Publ. No. 200, Washington, D. C. 1051 pp., illustrated. 1950.

\$3.00.

Flora of Illinois, by George Neville Jones. Second edition. Amer. Midl. Nat. Monogr. No. 5, University of Notre Dame Press, Notre Dame, Indiana. 368 pp. 1950. \$4.25.

A Manual of the Flowering Plants of California, by Willis Linn Jepson. Reprinted. University of California Press, Berkeley.

1238 pp., illustrated. 1951. \$5.00.

Drawings of British Plants, by Stella Ross-Craig. Part IV, Resedaceae, Cistaceae, Violaceae, Polygalaceae, Frankeniaceae. G. Bell & Sons Ltd., London. 26 pl. 1950. 5s. net.

Dictionary of the Flowering Plants and Ferns, by J. C. Willis. Sixth edition, reprinted. University Press, Cambridge. 752 pp.

1951. \$3.75.